

Return from the Lost: Rediscovery of the Presumed Extinct *Leptosolena* (Zingiberaceae) in the Philippines and its Phylogenetic Placement in Gingers

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The genus *Leptosolena* currently accepted as monotypic and endemic to the Philippines, has been considered as an imperfectly known genus due to the description based on insufficient herbarium materials for describing floral characters and no recent collection. Our rediscovery of *L. haenkei* has made it possible not only to describe the species in more depth from fresh materials and to compare with the uncertain second species, *L. insignis*, more precisely, but to clarify the phylogenetic position among Zingiberaceae with molecular data. Our results support the former treatment that *L. haenkei* and *L. insignis* are conspecific, resulting in *L. insignis* as a later synonym. The lectotype of *L. haenkei* is chosen among Haenke's historical collections deposited at PR and PRC. Results from DNA sequence data of the ITS and *matK* loci demonstrate that *Leptosolena* forms a clade with *Vanoverberghia* and *Alpinia* species from the Philippines and Oceania.

Key words: ITS, lectotypification, *Leptosolena*, *Leptosolena haenkei*, *matK*, molecular phylogeny, Philippines, rediscovery, Zingiberaceae

The genus *Leptosolena* C. Presl (Zingiberaceae) endemic to Northern Luzon, Philippines, comprises only one species, *L. haenkei* C. Presl as currently accepted (Larsen *et al.* 1998). *Leptosolena* is outstanding in Zingiberaceae by the large flowers with extremely long and slender corolla tube which are exerted from the calyx for more than half their

length (Smith 1990). The taxonomic position of this curious member of Zingiberaceae is always controversial. Bentham (1883) and Burtt & Smith (1972) mentioned a possible close affinity with *Burbridgea* which shares very short filament and smaller labellum than corolla lobes with *Leptosolena*. Schumann (1904) based on Presl (1827)'s

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† Professor Ken Inoue was killed by accident during field work in Sakhalin. The present paper is dedicated for the inspiring memory of the late Professor Inoue.

description and line drawing transferred *Leptosolenia* under the genus *Alpinia* L., subgenus *Autalpinia* K. Schum. and established section *Leptosolenia* (C. Presl) K. Schum. He changed suffix of “*Leptosolenia*” into “*Leptosolenia*” probably due to following the orthodox Latin word formation from the Greek word “lepto-solen” meaning “slender pipe.” Ridley (1909) recognized *Leptosolenia* as a distinct genus considering alliance with *Hedychium* which shares long corolla tube with *Leptosolenia*. Burt & Smith (1972) pointed out that *L. haenkei* is unlike any other *Alpinia* species because the inflorescence lacks bract and bracteole, and the corolla tube is extremely long and narrow, thus suggesting to maintain *Leptosolenia* at generic level pending more critical study. Larsen *et al.* (1998) mentioned this genus as “A poorly known genus, endemic to the Philippines, Luzon, with *L. haenkei* as the only species.” Kress *et al.* (2002) proposed a new suprageneric classification of Zingiberaceae based on molecular data, although *Leptosolenia*, good tissue materials being not available, was tentatively placed under subfamily Alpinioideae Link, tribe Alpinieae A. Rich. based on morphological features.

In 1906, Ridley described the second species of the genus *Leptosolenia insignis* Ridl. based on A. D. E. Elmer’s specimens collected at Twin Peaks (in Municip. Tuba near Baguio City), Benguet Province in Northern Luzon (Ridley 1906). But Merrill (1925) rendered the species synonym of *L. haenkei* without any specific reasons. Judging from Ridley’s diagnostic characters, *L. insignis* seems quite distinct. Nevertheless, no reconsideration has been made to date. The third species *L. auriculata* appeared in Elmer (1939). But the article is just a kind of a personal list of unpublished names. Elmer (1939) stated, “The following numbers of my collection with unpublished new names should be considered published specific names as indicated below with their authors,” “17977-*Leptosolenia auriculata* is *Leptosolenia haenkei* Presl.” Therefore we will

not discuss about *L. auriculata* in the present study.

Leptosolenia haenkei was recollected from the valley slope along Chico River near Bontoc, Mountain Province, Northern Luzon by the first author and Leonardo Co in May 2002. The rediscovery of the plants in full bloom in its natural habitat has made it possible not only to describe the species in more depth and to compare with an uncertain second species, *L. insignis* Ridl., but to carry out DNA-sequencing studies to clarify the phylogenetic relationship of this genus with other genera of subfamily Alpinioideae of the Zingiberaceae.

Materials and Methods

The field collections and tissue samples were made in the Mountain Province of Northern Luzon. Herbarium material examined was from the following institutions: AAU, BR, E, GH, KYO, L, P, PNH, PR, PRC, PUH, SING, and US.

Data from previous investigations of the phylogenetic relationships within the family Zingiberaceae (Kress *et al.* 2002) were used to determine the evolutionary position of the genus *Leptosolenia* in the subfamily Alpinioideae. In total 51 species were analyzed, including three outgroup taxa in the genus *Siphonochilus*, 46 taxa previously sequenced in the Alpinioideae, and the two new taxa. Comparative sequence data of the internal transcribed spacer (ITS) loci and *matK-trnK* flanking intergenic spacer regions were generated for *L. haenkei* following the procedures of Kress *et al.* (2002), including DNA extraction, amplification, and sequencing.

Phylogenetic analyses followed the same procedures as Kress *et al.* (2002). Maximum parsimony analyses of the ITS and *matK* sequence data were conducted using PAUP*4.0 (Swofford 1998) with unweighted characters and 500 random-sequence-addition replicates, saving all shortest trees under TBR Branch Swapping, STEEPEST DESCENT off, MULTREES on, COLLAPSE

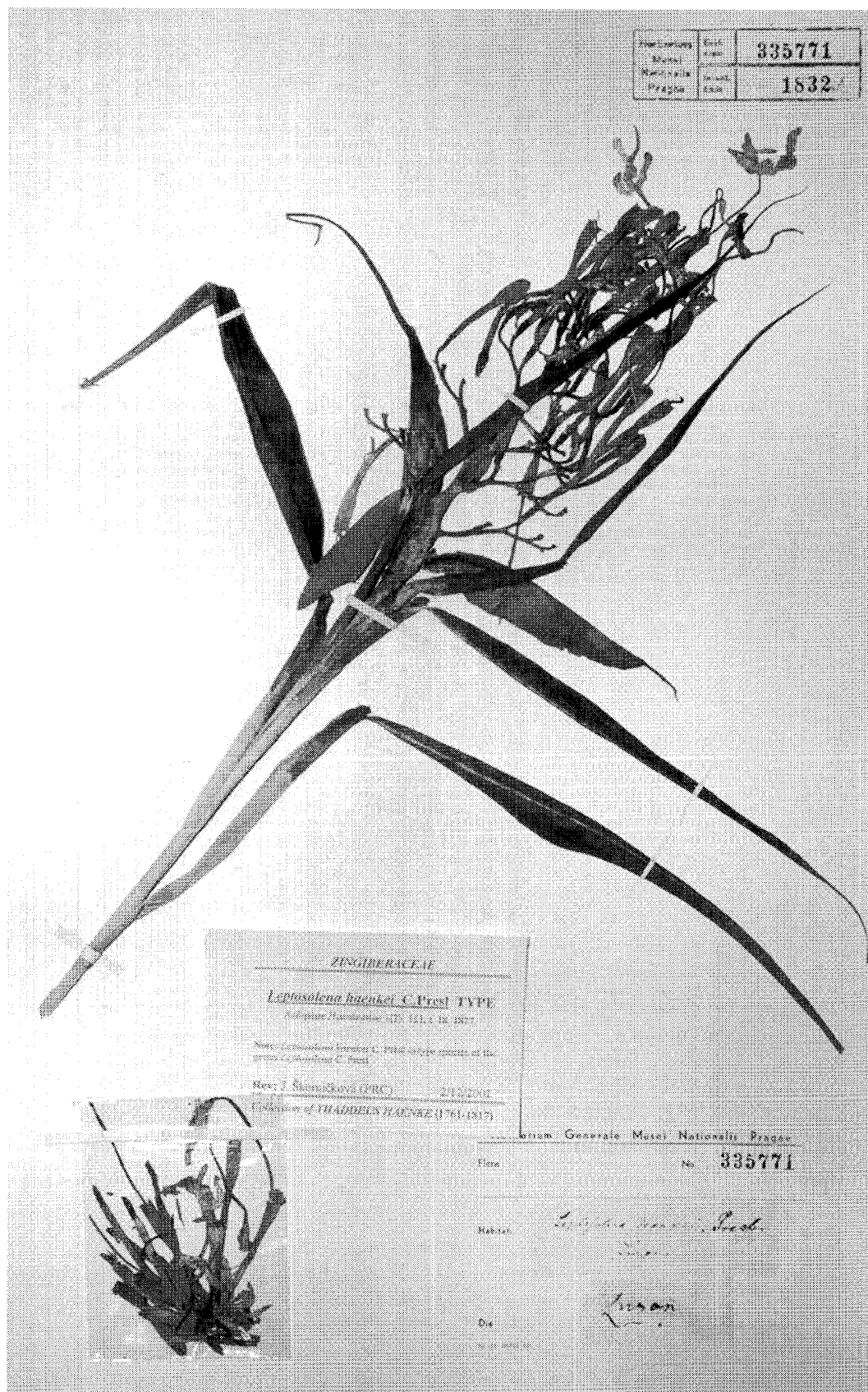


FIG. 1. The lectotype of *Leptosolena haenkei* C. Presl (*T. Haenke s.n.*, sheet no. 335771-1832A, PR) with K. B. Presl's handwriting (upper portion, identified by B. Skočdoplová, PR).

branches if maximum length is zero. Bootstrap analyses were conducted using PAUP*4.0 with ten random addition replicates, TBR branch swapping, for 100 bootstrap replicates. The data sets for each gene region were analyzed separately and then, following the total evidence approach for multiple data sets, combined.

Results and Discussion

Taxonomic comparison between Leptosolena haenkei and L. insignis

We first examined the concordance of character figures in the text of Presl's (1827) original description of *Leptosolena haenkei*, attached illustration in Presl (1827) with notes as drawn in actual specimen size, and our measurement in Haenke's original materials (four sheets) deposited at PR and PRC. (1) In pedicel, written as pediceled in Presl's text, pediceled in illustration, pediceled in original materials we measured. (2) In calyx length, 3.8 cm in text, 4.5 cm in illustration, 4.2 - 5 cm in original material (10 flowers measured). (3) In corolla tube length, 7.5 cm in text, 9.1 cm in illustration, 8 - 9 cm in original material (five flowers measured). (4) In corolla lobe length, 1.5 cm in text, 1.4 cm in illustration. (5) In anther crest, diverged in text, not developed in illustration. (6) In leaves, 25 - 27.5 cm×2.5 cm in text, 20 - 31 cm×2 - 2.8 cm in original material.

According to Ridley (1909), the differences between the two species are as follows.

Flowers pediceled, calyx 1.5 cm long, corolla tube 7 cm long, corolla lobe 1.2 cm long, anther crest not prolonged, leaves lanceolate (30×2.2 cm)
*Leptosolena haenkei*
 Flowers sessile, calyx 6 cm long, corolla tube 12 cm long, corolla lobe 2 cm long, anther crest large, leaves linear (25×1 cm).....*L. insignis*

First of all, Ridley's description in calyx length of *Leptosolena haenkei* as 1.5 cm is very much likely to be a mistake of 1.5 inches, because in Presl's original description it was described as "*sesquipollicaris*" which means 1.5 inches. Haenke's specimens lie between Ridley's description of *L. haenkei* and *L. insignis*.

In the types of *Leptosolena insignis* (holotype, K, non vidi; isotype, NY, digital image seen; P, digital image seen; SING!; US, digital image seen; type location described in Turner (2000)), distinct pedicels could be recognized but too short to measure their length in the isotype at US, but they were obvious in the isotypes at P, SING, and NY. The measured characters are: calyx 7.2-7.8 cm long (five flowers measured, SING), corolla tube 12.7 cm (two flowers measured, SING), leaves 31×2 cm (NY), 30×1.6 cm (SING), 25×2 cm (US). All leaves were mounted in condition folded in half from midrib, but the leaf width is almost double the figure which Ridley described. Then the diagnostic characters from our recent collection from Northern Luzon, Philippines were measured (five flowers from three plants preserved in spirits were measured, leaves were separately collected from the middle of the pseudostems); calyx 7.3-7.8 cm, corolla tube 11.0-11.5 cm, leaves 42-45×3-3.2 cm. We confirmed the presence of distinct pedicel (4 mm long) and a little developed anther crest.

In the other specimens examined, calyx length are 6.5cm (*Vanoverbergh s.n.*, BR); 6.0cm (*Santos 5674a*, L); 6.8cm (*Steiner 2198*, L); 5.5cm (*Fox 230*, GH). Corolla tube are 10.7cm (*Vanoverbergh s.n.*, BR); 10.6cm (*Santos 5674a*, L); 10.9cm (*Fox 230*, GH).

Our recent collection matches well with neither of these two species' descriptions, or rather with a mixture of these two descriptions; which means that *Leptosolena haenkei*, *L. insignis*, and our recent collection are conspecific, resulting in *L. insignis* as later synonym. The character figures derived from

herbarium specimens of *Leptosolenia* other than types which lie in-between support that *L. haenkei* and *L. insignis* are conspecific. To avoid confusion, we provide a more accurate description of *L. haenkei* based on our recent fresh collection together with character information observed in all examined herbarium specimens.

The lectotypification of Leptosolenia haenkei C. Presl

As for Haenke's specimens were distributed to about 20 herbaria (Stearn 1973) which includes B, BM, BR, F, G, GH, GOET, K, L, LE, M, NY, and W (Skočdoplová 1995). For inquiry for locating Haenke's original materials, only negative responses were derived from B, BR, F, GH, L, M, NY, and W. As for Haenke's specimens of *Leptosolenia haenkei*, Schumann (1904) stated that "type specimen has probably been lost because it doesn't exist anymore in German University or Bohemian Museum at Prague." But Haenke's collection of *L. haenkei* are currently extant at PRC (Charles University which was formerly called German University; one sheet) and PR (three sheets) even though Schumann actually confirmed some other Zingiberaceae specimens (e.g. *Alpinia mollis* C. Presl, *Alpinia brevifolius* C. Presl, *Kolowratia elegans* C. Presl) at PRC judging from his determinavit slips as "Bearbeitet für das Pflanzenreich" (Treated for the Pflanzenreich). Nevertheless, the misunderstanding of the type as lost as suspected in Burt & Smith (1972) who believed Schumann's note prevailed until recently. Although Presl didn't cite any particular specimens in his protologue of *L. haenkei* in *Reliquiae Haenkeanae*, Haenke's extant collection of the species at PR and PRC should be considered as elements of original material. Here we select the most well-represented specimen as the lectotype of *L. haenkei* (Fig. 1).

***Leptosolenia haenkei* C. Presl, Reliq. Haenk. 1: 111, t.18 (1827); Petersen, in Engl., Pflanzenf.**

2 (6): 23 (1889); Ridl., Philipp. J. Sci. C. Bot. 4: 181 (1909); Merr., Enum. Philipp. Fl. Pl. 1: 236 (1925); Larsen et al., in Kubitzki, Fam. Gen. Vasc. Pl. 4: 492 (1998). -*Alpinia leptosolenia* K. Schum., Pflanzenr. IV. 46: 312 (1904), with incorrect author citation as (C. Presl) K. Schum. non A. *haenkei* C. Presl (1832). -Lectotype: Philippines, Luzon, *T. Haenke s.n.* (PR, sheet no. 335771-1832A [Fig. 1], iso-: PR, sheet nos. 335771-1832B, 335771-1832C; PRC). (here designated)

Leptosolenia insignis Ridl., Publ. Bur. Sci. Govt. Lab. 35: 84 (1906); Ridl., Philipp. J. Sci. C. Bot. 4: 181 (1909); Elmer., Leaflet Philipp. Bot. 8: 2907 (1915). -Type: Luzon, Benguet Prov., Twin Peaks, A. D. E. Elmer 6428 (K, non vidi; NY [digital image!], P [digital image!], SING!, US [digital image!]).

Leptosolenia auriculata Elmer, Leaflet Phil. Bot. 10: 3808. (1939), nom. nud. -Specimen cited: cultivated at Los Banos, Laguna Prov. Luzon A. D. E. Elmer 17997 (F, non vidi; L, non vidi; NY, non vidi; W [digital image!]).

Perennial, evergreen herb. *Pseudostems* erect, not drooping toward the top, 280-330 cm long. *Rhizomes* elongate, with ca. 20 cm interval between neighboring pseudostems. *Plane of distichy* of leaves is perpendicular to rhizome. *Leaves* glabrous, sessile, linear, numerous, ca. 66-75 leaf blades per pseudostem at flowering season, base cuneate-rounded, apex caudate-attenuate, 42-45 × 3-3.2 cm in the middle of pseudostem. *Ligules* glabrous, as an erect pair of auricles, oval, rounded at tips, 7 mm long. *Inflorescence* glabrous, paniculate, 7-11 cm long, terminal on the pseudostem, with 2-4 brown persistent inflorescence bracts. *Lower cincinni* have 5-6 flowers with distinct pedicels which are 4 mm long. *Floral bracts* subtending cincinni, and bracteoles absent. *Calyx* tubular, irregularly 2-3 lobed shortly, split deeper on one side, 4.2-7.8 cm long. *Corolla* tubes long and narrow, white, 8.0-12.7 cm long.

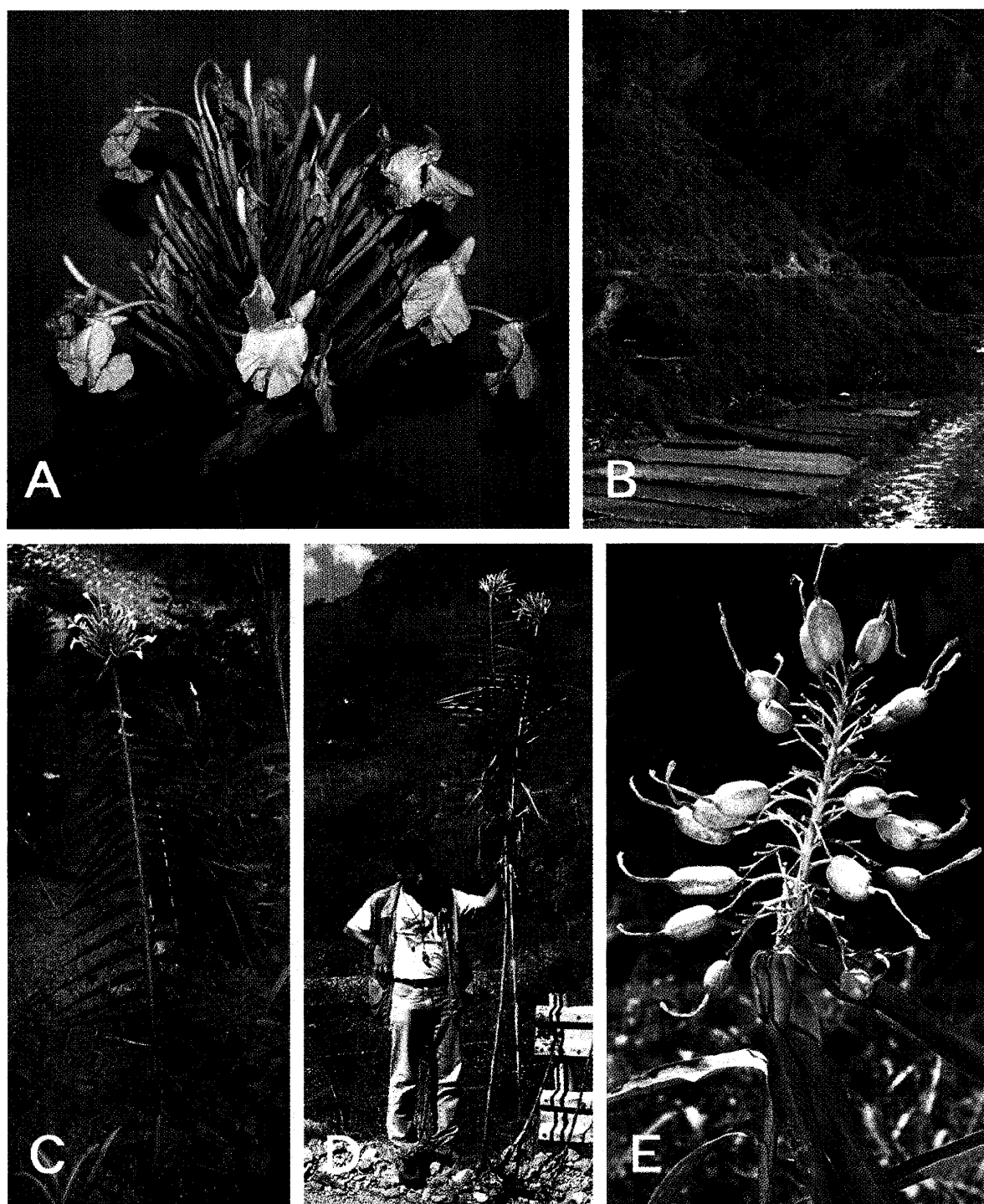


FIG. 2. A: Inflorescence of *Leptosolena haenkei* in full bloom (at 2000 hr). B: Habitat of *L. haenkei*. C: Upper portion of flowering pseudostem of *L. haenkei* in its habitat. D: Whole plant of *L. haenkei*. E: Infructescence of *L. haenkei*. A, C, D (Funakoshi & Co 2006), E (Funakoshi 2025).

it with *Alpinia elegans*, *A. luteocarpa*, and the two species of *Vanoverberghia*. However, strong support (bootstrap value = 93%) is provided for uniting it in a clade with *Etlingera* and *Hornstedtia* as well as with several species of *Amomum* (bootstrap value =

95%).

The results of the molecular analyses suggest that *Leptosolena* evolved in a clade with other taxa in subfamily Alpinioideae tribe Alpinieae now distributed in the Philippines (e.g., *Vanoverberghia*

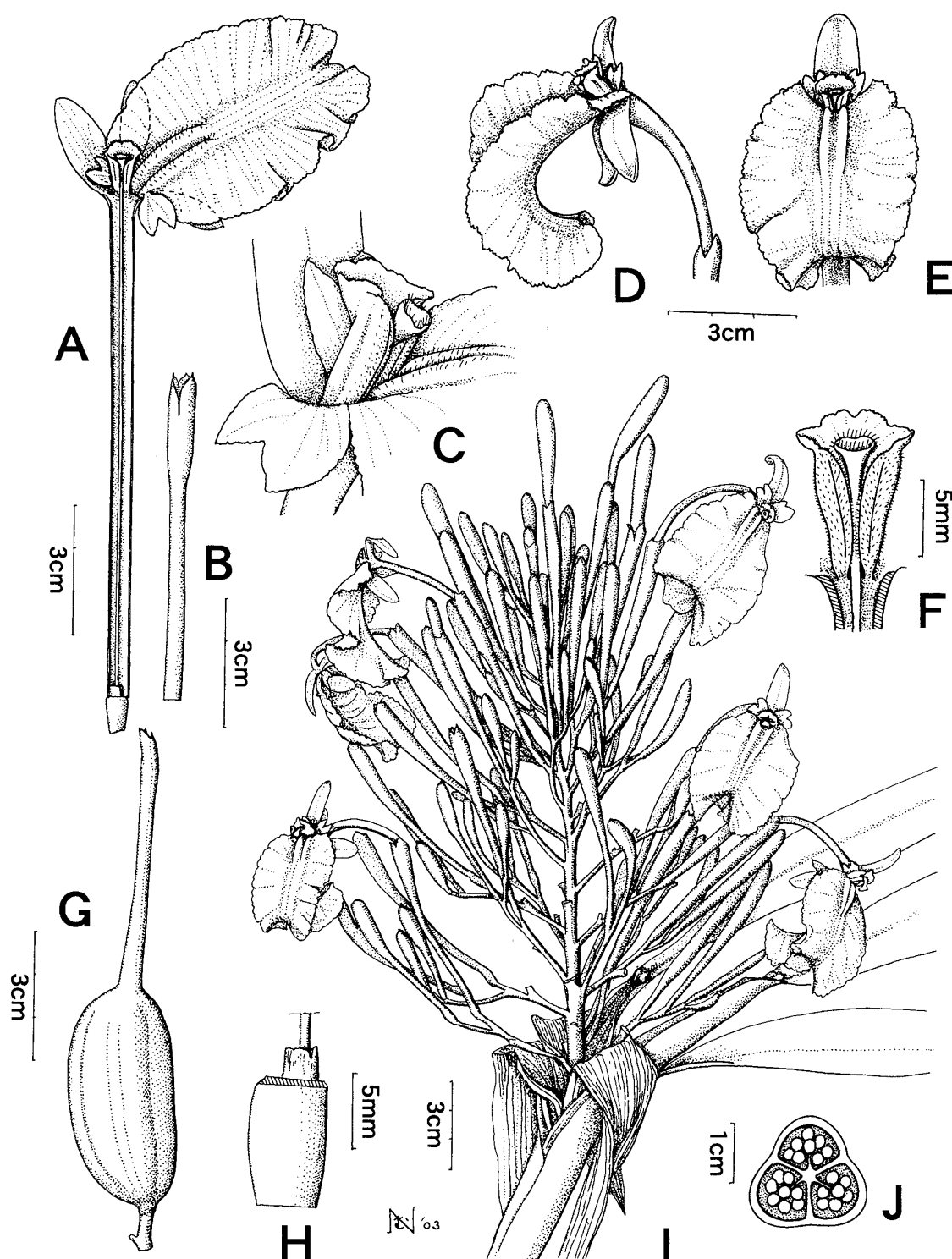


FIG. 3. *Leptosolena haenkei* C. Presl. A-F, H-I (Funakoshi & Co 2006), G, J (Funakoshi 2025). A: flower, dissected. B: calyx. C: close-up of labellum base. D: flower, side view. E: flower, frontal view. F: anther and anther crest. G: capsule. H: nectary and ovary. I: inflorescence. J: transverse section of capsule.

Corolla lobes oblong-ovate, apex obtuse, 2 cm long. *Lateral staminode* petaloids, obcordate, apex of the two lobes subacute, 7 mm long. *Labellum* oval, erose-crested, fragile, recurved, white with no nectary guide observed to human naked eyes, $4.7\text{--}5.1 \times 3.5\text{--}4.0$ cm and palate pubescent. *Filament* almost unable to be recognized. *Anther* 8 mm long with a little developed anther crest. *Stigma* cup-shaped, with hairs along the edge of the hollow. *Ovary* 3-locular, axial placentation, 8×5 mm. *Capsules* glabrous, oblong, slightly trigonous, containing numerous arillate seeds, with persistent calyx at apex, $4.6\text{--}5.1 \times 2.0\text{--}2.5$ cm excluding persistent calyx length. *Seeds* subglobose, irregular in shape, ca. 2 mm in diameter.

Distribution: PHILIPPINES, Northern Luzon (Benguet, Cagayan, Ilocos Norte, La Union, Mountain Prov., Nueva Vizcaya, Zambales) (addition made to Merrill [1925]); alt. 300–1300m.

Habitat and Ecology: Abundant on sunny rocky slopes where even dominant *Pinus kesiya* forest are unable to be sustained (Fig. 2B). This species is characterized by the nocturnal anthesis; its labellum starts expanding a few hours before sunset. This phenomenon frequently led the incorrect description of the flower. In Ridley (1906), it was described as “Lip fleshy, elongate, 1 inch long,” but actually the labellum looks like a wrinkled fragile paper reaching ca. 5 cm long after its full expansion after sunset (Fig. 2A). The flower also emits a sweet fragrance during its anthesis. Those characteristics together with snow white flower color, no visible nectary guide, long (ca. 11 cm) and narrow corolla tube and almost no filament unlike *Hedychium* might imply the pollination by specialist like non-hovering moths with a very long proboscis. It is also worth to mention about the unique fruit; relatively big fruits (Fig. 2E, ca. 5×2.5 cm) contain numerous arillate seeds which taste sweet and sour. This probably means seed dispersal by fruit bats, but the conclusion must await further field observation.

Other specimens examined: PHILIPPINES, Supan, Mountain Prov., Luzon, Jun. 4, 1911, *M. Vanoverbergh s.n.* (BR); Bauan - Mt. Tabuan, Cagayan Prov., Luzon, May, 1929, *M. Ramos 77052* (NY, SING); Villar, Mt. Pinatubo, Zambales Prov., Luzon, alt. 350 m, May 18, 1948, *R. B. Fox 230* (GH, PNH); Sitio Dandanak, Barrio Bana-aw, Municip. Besao, Bontoc Subprov., Mountain Prov., Luzon, alt. 2600 ft, May 5, 1953, *J. V. Santos 5674a* (L, PUH); road Bontoc - Mt. Data, Mountain Prov., May 14, 1961, *M. L. Steiner 2198* (L); Brgy Alab, Municip. Bontoc, Mountain Prov., Luzon, alt. 1100 m, May 3, 2002, *H. Funakoshi & L. L. Co 2006* (AAU, E, PUH, KYO, US); Brgy Balili, Municip. Bontoc, Mountain Prov., alt. 940 m, Sept. 29, 2002, *H. Funakoshi 2025* (E, GH, PUH, KYO, L).

Phylogenetic placement of Leptosolena haenkei in the Zingiberaceae

ITS – The analysis of the ITS sequence data resulted in six equally parsimonious trees of 743 steps (consistency index [CI] = 0.479; retention index [RI] = 0.750; rescaled consistency index [RC] = 0.359; Fig. 4). *Leptosolena* is strongly supported (bootstrap value = 96%) as a member of a clade containing species of *Alpinia*, *Vanoverberghia*, *Etlingera*, and *Hornstedtia* although there is only poor bootstrap support for its closest relatives within this clade.

matK – The analysis of the *matK* region (coding and noncoding) resulted in 120 equally parsimonious trees of 518 steps (CI = 0.703; RI = 0.882; RC = 0.6230; Fig. 5). *Leptosolena* is strongly supported (bootstrap value = 93%) as sister to *Alpinia vittata* but only has weak bootstrap support as a member of the clade made-up of *Alpinia elegans*, *A. luteocarpa*, and the two species of *Vanoverberghia*. Only poor support is provided for uniting it in a clade with *Etlingera* and *Hornstedtia*.

Combined data set – The analysis of the combined ITS and *matK* sequence data resulted in 64 equally parsimonious trees of 1,286 steps (CI = 0.564; RI = 0.803; RC = 0.453; Fig. 6). *Leptosolena* is weakly supported (bootstrap value = 59%) as sister to *Alpinia vittata* with poor support in uniting

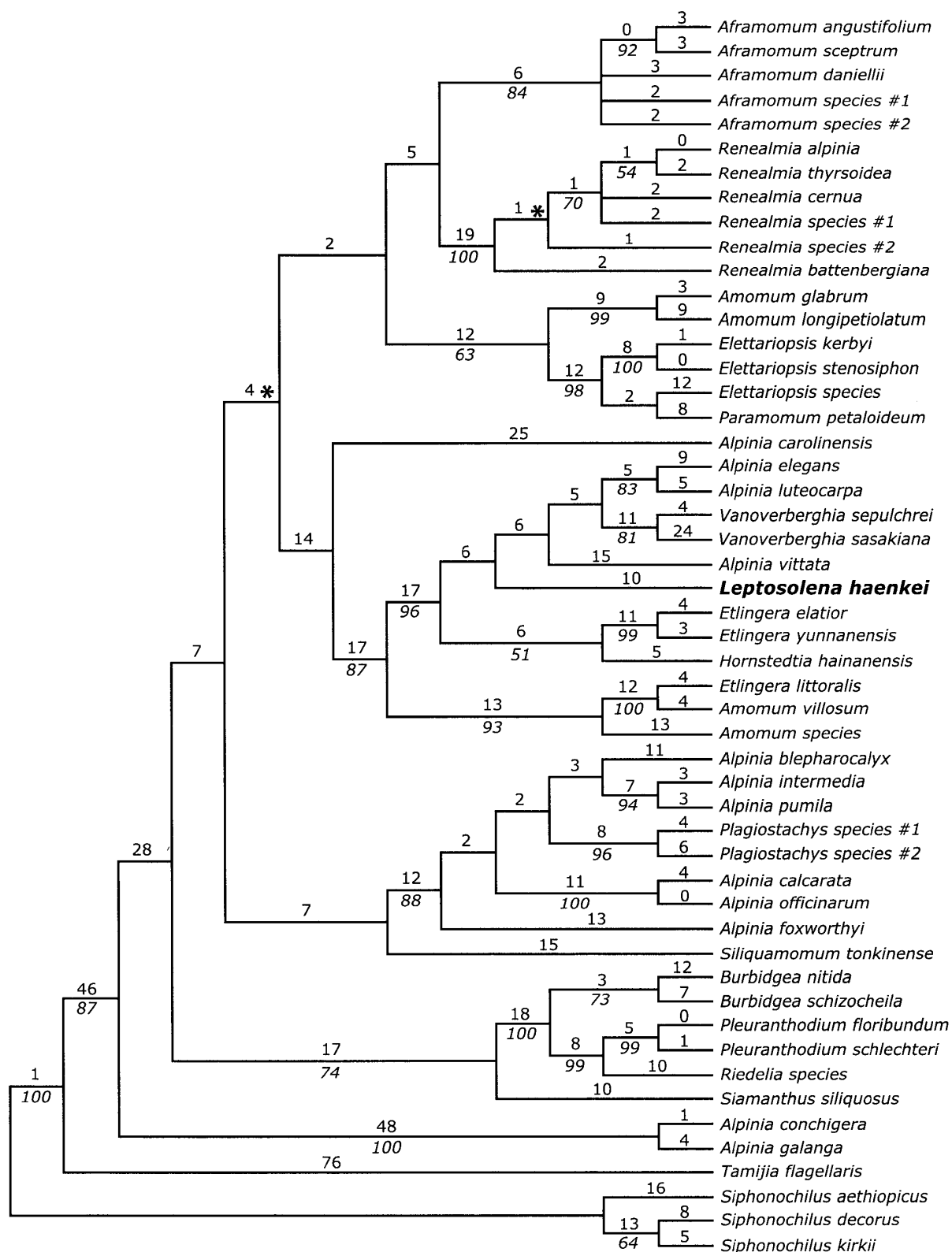


FIG. 4. One of the six equally parsimonious trees of subfamily Alpinioideae in the analysis of the ITS sequence data (length = 743; consistency index = 0.479 excluding uninformative characters; retention index = 0.750; and rescaled consistency index = 0.359) showing branch lengths (above the line) and bootstrap values (below the line if $\geq 50\%$). Asterisks indicate nodes that collapse in the strict consensus tree.

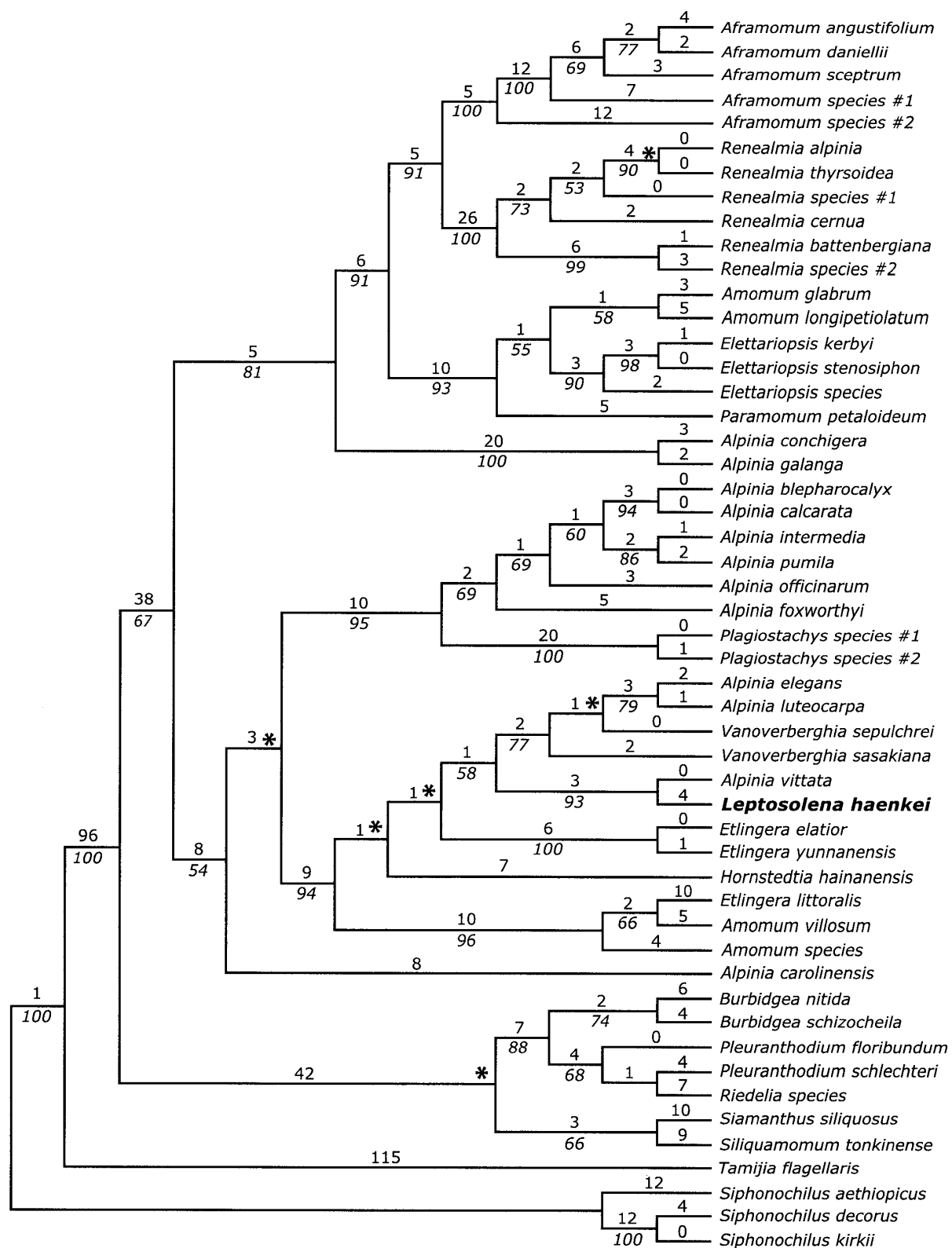


FIG. 5. One of the 120 equally parsimonious trees of subfamily Alpinioideae in the analysis of the *matK* region (coding and noncoding) sequence data (length = 518; consistency index = 0.703 excluding uninformative characters; retention index = 0.882; and rescaled consistency index = 0.620) showing branch lengths (above the line) and bootstrap values (below the line if ≥ 50%). Asterisks indicate nodes that collapse in the strict consensus tree.

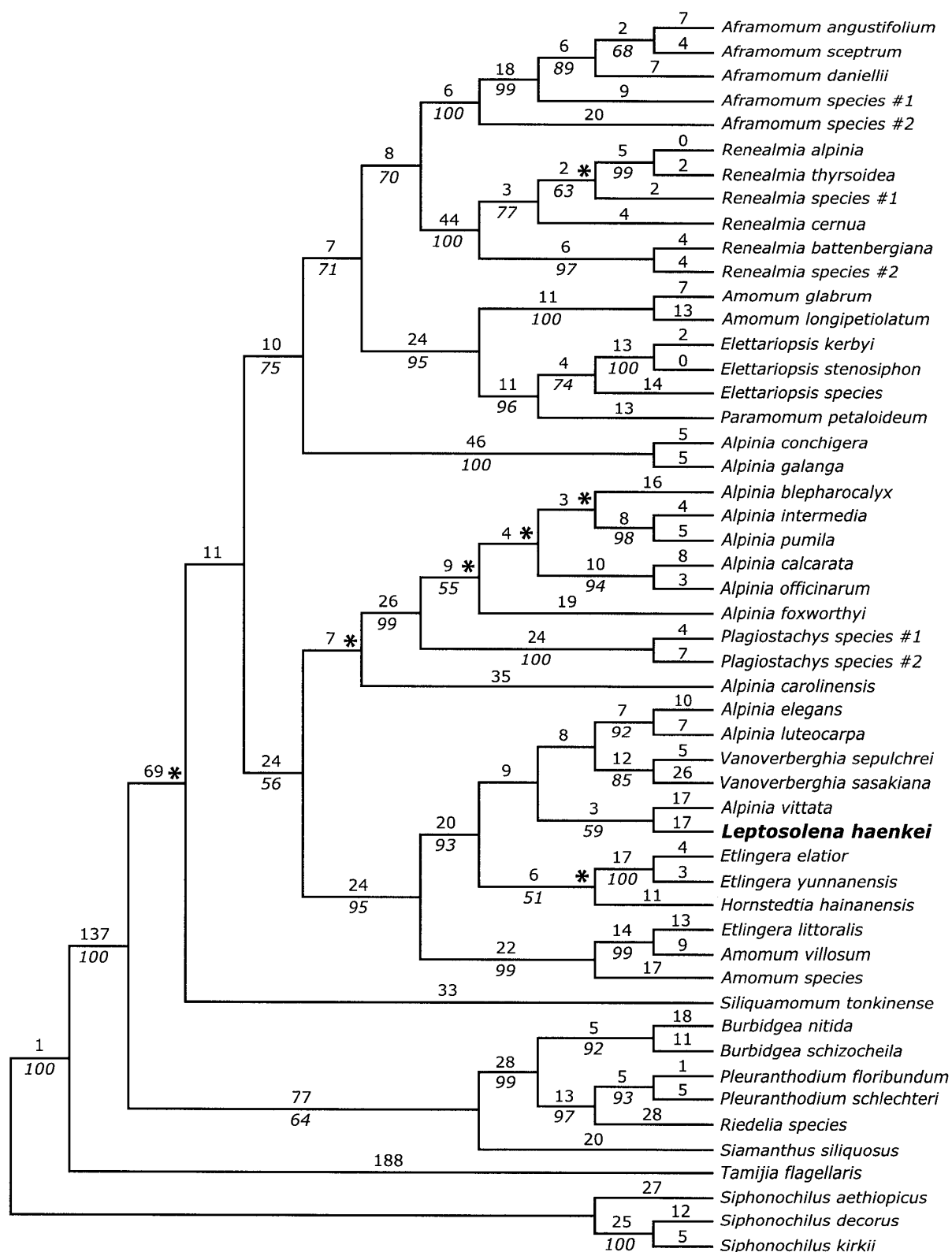


FIG. 6. One of the 64 equally parsimonious trees of subfamily Alpinioideae in the analysis of the combined ITS and *matK* region sequence data (length = 1,286; consistency index = 0.564 excluding uninformative characters; retention index = 0.803; and rescaled consistency index = 0.453) showing branch lengths (above the line) and bootstrap values (below the line if ≥ 50%). Asterisks indicate nodes that collapse in the strict consensus tree.

TABLE 1. List of species used in the phylogenetic analyses of the Zingiberaceae. Voucher number, location, country of origin, and GenBank accession number of gene sequences are provided.

Taxon name	Voucher information: collector, number, and herbarium location	Country of origin	GenBank accession number for ITS sequences	GenBank accession number for matK sequences
<i>Leptosolena haenkei</i> C.Presl	Funakoshi & Co 2006, US	Philippines	AY742331	AY742390

sepulchrei, *Alpinia luteocarpa*, and *A. elegans*) and Oceania (*A. vittata*) and is also related to species of the genera *Amomum*, *Etilingera*, and *Hornstedtia* (Kress *et al.* 2002). Contrary to the notion of Benth (1883) and Burt & Smith (1972), *Leptosolena* is only distantly related to the Bornean genus *Burbridgea* in tribe Riedelieae. No evidence supports Ridley's (1909) contention that this genus is closely related to *Hedychium* placed in subfamily Zingiberoideae Haask. (Kress *et al.* 2002).

In our analysis the genus *Leptosolena* is sister to *Alpinia vittata*, but is quite unlike its closest relative in morphological characters; viz. 11 cm vs. 2 cm in corolla tube length, no floral bract and bracteole vs. conspicuous bract and tubular bracteole, a well-developed labellum vs. an inconspicuous labellum that is almost the same size as the corolla lobes. *Alpinia elegans* and *A. luteocarpa*, both belonging to sect. *Kolowratia* endemic to the Philippines (Smith (1990), Funakoshi unpublished data), have some characteristics in common with *Leptosolena* in their nocturnal anthesis and relatively large fruits with "sweet and sour" arillate seeds (Funakoshi unpublished data). *Vanoverberghia*, another interesting representative of the Zingiberaceae in the Philippines, is quite different from *Leptosolena* in the conspicuous bracts subtending one flower, the deeply bilobed labellum basally connate to the corolla lobes, and the channeled filament enclosing the style. Other species (*Etilingera elatior*, *E. yunnanensis*, *Hornstedtia hainanensis*) included in the same clade with *Leptosolena* differ in possessing basal inflorescences in contrast to terminal inflorescences on leafy shoots in *Leptosolena*, *Alpinia*, and *Vanoverberghia*. As mentioned earlier, the

extremely long and narrow corolla tube, the lack of floral bracts and bracteoles, and especially the petaloid lateral staminodes, which are exceptional in subfamily Alpinioideae, make *Leptosolena* a readily recognizable genus in Zingiberaceae.

The phylogenetic placement of *Leptosolena* in a clade containing species of the highly polyphyletic genus *Alpinia* is problematic for delimiting generic boundary in this tribe. Although *Leptosolena* is morphologically distinct, it is yet undetermined how species can be combined into monophyletic genera in these clades. Further analyses of additional taxa using molecular characters and more in-depth studies of morphological character variation are warranted before new generic boundaries can be established.

The authors are grateful to Leonardo Co (PUH) for giving full facilities for the field survey in the Philippines. We greatly appreciate a deep insight on the technical term given from Kai Larsen (AAU) and Mark Newman (E). We wish to express our gratitude to Shutaro Nishihara, Mutsuko Nakajima, and Ida Lopez for preparing Fig. 2, Fig. 3, and Figs. 4-6, respectively. Our sincere thanks also go to the directors and curators of B, BO, BR, F, GH, L, M, NY, P, PNH, PR, PRC, PUH, SING, US, and W for the permission to examine the specimens or for the search for locating specimens or for providing Web sites to see the digital images of type specimens. We acknowledge Jin Murata (TI), Hideki Nakai, Hidetoshi Nagamasu (KYO), and Masanao Honda for providing invaluable comments on the manuscript.

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Received October 15, 2004; accepted January 13, 2005